

PHYSIOLOGICAL ECOLOGY AND INTERTIDAL ZONATION IN
LIMPETS (*ACMAEA*): A CRITICAL LOOK AT
"LIMITING FACTORS"¹

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The striking intertidal gradient from marine to terrestrial physical conditions is correlated with an equally obvious spatial partitioning of the habitat by groups of animals. This has repeatedly given rise to the assumption that terrestrial physical factors, acting during tidal emersion, determine the upper range limits of intertidal populations. This assumption is elevated to the level of a hypothesis in this study and tested with scientific rigor. If conditions in the physical environment serve as "limiting factors," determining the partitioning of the intertidal, it should be demonstrable that (a) interspecific differences in physiological tolerances exist and permit differential exploitation of the habitat, and (b) conditions in the micro-environment of the animals exceed the physiological tolerances at the fringes of ranges and, by causing mortality, prevent range extension.

The conditions most often assumed to serve as "limiting factors" are high temperatures (Huntsman and Sparks, 1924; Broekhuysen, 1940; Allanson, 1958; Read and Cumming, 1967; and many others) and/or desiccation (Test, 1945; Shotwell, 1950b; Haven, 1970). The assumption rests on two sorts of correlations: those between physiological tolerances and zonation, and those between fair weather and death or disappearance of animals in the field.

A relationship between laboratory physiological tolerances and zonation is probably the most frequently demonstrated facet of intertidal biology. Numerous workers have shown that, in comparison with organisms living lower, high-intertidal animals tend to have higher lethal temperatures (Evans, 1948; Southward, 1958; Fraenkel, 1968; Sandison, 1968; Hardin, 1968; Davies, 1970), higher desiccation tolerances and lower desiccation rates (Colgan, 1910; Broekhuysen, 1940; Allanson, 1958; Brown, 1960; Bock and Johnson, 1967), and greater tolerance of osmotic extremes (Broekhuysen, 1940; Arnold, 1957; Brown 1960; Davies, 1969). The high tolerances of high-intertidal animals, and some of the physiological effects of exposure, have been especially well documented in the careful and detailed work of Kensler (1967) with crevice-dwelling invertebrates, Foster (1971) with barnacles, and Davies (1969, 1970) with British limpets (*Patella*). Unfortunately, even in these studies there is a paucity of data concerning the extremes of the microclimates experienced by the animals in the field. Without a demonstration that physical conditions in the field exceed the physio-

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logical tolerances of the animals, it cannot be stated with confidence that physical factors are limiting. In actuality, in those studies where field measurements are given, body temperatures (Southward, 1958; Hardin, 1968; Davies, 1970; Markel, 1971), and desiccation level or osmotic stress (Segal and Dehnel, 1962; Davies, 1969; Boyle, 1970), are always well below the lethal limits as determined in the laboratory.

Occasionally, observers have noted the death or disappearance of animals from the upper ends of intertidal ranges, usually during warm, dry weather, often when midday low tides coincided with minimal wave splash (Orton, 1933; Hodgkin, 1959; Frank, 1965a; Sutherland, 1970). However, since no measurements of field microclimates or condition of animals were made at the time of these "kills," again it is impossible to establish a casual relationship between physical conditions and the proximal cause of death. For example, the finding of dead, dry animals in the field can mean either that the animals were killed by desiccation, or that the animals dried out because they were dead.

In short, despite countless studies showing how intertidal animals are adapted to live where they do, the actual importance of physical factors in limiting the distribution of populations remains unclear. To shed additional light on this issue, an intensive study has been made of the physiological ecology and zonation of five species of limpets (*Acmaea*) from the central California coast. All five species are similar in their morphology and basic biology, but occupy different zones and microhabitats; thus they present a convenient system in which to compare the effects of physical factors. The hypothesis that the upper limits of their distributions are determined largely by physical environmental factors has been tested according to the criteria mentioned earlier. Laboratory tolerances to the environmental conditions likely to produce stress in the field have been measured, to determine if interspecific differences allow exploitation of different portions of the intertidal gradient. Concurrently, the extremes of the same environmental conditions occurring in the microhabitats of each species have been monitored for a period of three years, to determine if these conditions ever exceed the tolerances of the limpets and, by causing mortality, limit their ranges.

MATERIALS AND METHODS

The five species of limpets used all occur commonly on rocky central California shores. Three of the species normally inhabit the bare rocks of the splash zone (Zone I of Ricketts and Calvin, 1962)—from about 5 feet above mean lower low water (MLLW) to the limit of high-water splash. *Acmaea digitalis* Eschscholtz, 1833, is a small (1–2 g) greenish-gray to eroded brown limpet occupying primarily vertical or overhanging surfaces (Haven, 1970). On cliffs receiving large amounts of spray this species ranges higher than any other, up to 30 feet above MLLW. *Acmaea scabra* (Gould, 1846) is a small (1–2 g) heavily ribbed gray to white limpet occupying primarily horizontal surfaces fully exposed to the sun (Haven, 1970). It returns regularly to the same orientation on the same scar on the rock surface, or "homes," and the shell margin grows to fit the home scar precisely. *Acmaea persona* Eschscholtz, 1833, is a large (to 10 g), smooth olive-shelled limpet, found in dark crannies and under boulders, sheltered from

the sun. It is negatively phototactic, moving and feeding only during the night (Richardson, 1934; Ricketts and Calvin, 1962).

Two of the species are found among the scattered clumps of algae in the upper mid-tidal (Zone II of Ricketts and Calvin, 1962)—from about +4 to about +5 feet above MLLW at Bodega Head. *Acmaea pelta* Eschscholtz, 1833, is a high-peaked brown limpet, very variable in form, which typically reaches a maximum size of about 5 g. It is characteristically found among or under macroscopic algae on surfaces experiencing mild to moderate wave action, such as the walls of surge channels. *Acmaea testudinalis scutum* Eschscholtz, 1833, is a moderate-sized (2–4 g) limpet distinguished from the others by its extremely flat shell profile. It is characteristically found on the damp, shaded walls or boulders at the bottom of surge channels, or in tidepools.

The study was carried out at the University of California's Bodega Marine Laboratory, located on Bodega Head, Sonoma County, California, about 110 km north of San Francisco. The rocky shore at the Laboratory is composed of heavily jointed, extremely rugged diorite granite. The biotic zonation is in accord with the descriptions of Ricketts and Calvin (1962) for exposed rocky coast, though modified by wave action and the unevenness of the surface.

The weather is dominated by the cold Japanese current into which Bodega Head juts; water surface temperatures range from 9° C in May to 16° C in September. Mean daily maximum air temperatures range from about 10° C in January to about 20° C in late August; very rarely mild frosts occur on winter nights. Aside from winter rainstorms, bringing from 45 to 125 cm (average 76 cm) of rain per year, two principal types of weather occur at the Laboratory: considerable periods of fog and little wind, especially during the summer; and periods of sunny weather with high (30–100 km/hr) northwest winds. Occasionally there are days that are both clear and calm; rarely (probably less than 10 days each year) these conditions will be accompanied by air temperatures exceeding 20° C (based on local meteorological data analyzed by M. G. Barbour (University of California, Davis) and K. L. van der Laan (University of California, Berkeley); personal communication).

The tides at Bodega Head are of the mixed semi-diurnal type, with two unequal high and two unequal low tides each day. During the spring and early summer the lower low tide occurs during the morning hours and is followed by the lower high tide. At such times both Zone I and Zone II may remain exposed all day, being submerged only a few hours during the night. During these periods, maximum stresses are experienced by intertidal organisms, particularly if midday low tides occur on one of the rare warm days. Time of day of lower low water and expected submergence times through the year at the Bodega Marine Laboratory have been calculated by Sutherland (1970). When seas are calm, Zone I limpets may expect a maximum of 4 hours immersion once per day and a minimum of no immersion for several consecutive days during portions of the spring and early summer. In contrast, Zone II limpets may expect a minimum of 4 hours immersion at least once per day during these same periods.

Limpets were collected from rocky shores near the Laboratory, and as far north as the Russian River, about 13 km away. Capture was effected by a quick prying motion with the "limpet snatcher," a sawed off stainless steel table knife.

Those individuals which did not yield to the first effort were left, since experience showed that products of the second and subsequent tries were usually injured and unusable. Limpets were returned to the laboratory and placed under running sea water immediately after collection. All animals were used within 48 hours, with the exception of some *A. scabra*, which were maintained for several weeks on glass plates in a system providing two artificial tides of fresh sea water daily. Some food was provided in the form of microscopic algae growing on the plates. This regime permitted the growth of flat shell margins on *A. scabra*, which facilitated comparison with the other species in desiccation studies.

Field measurements were designed to evaluate the extremes of microclimates experienced by, or available to, the limpets. Measurement sites were selected accordingly; for instance, the majority of high-temperature data was collected in Zone 1 on the south-facing side of the cove adjacent to the Laboratory, between 12:00 and 15:00 on clear, calm, exceptionally warm days. During the relatively few hours of such hot periods, intensive searches were made for limpet microhabitats that received maximum solar radiation and were sheltered from wind and splash.

Temperatures of air (shaded) at 2 m and 1 cm above the rocks, rock surface temperatures, and limpet body temperatures were measured by two methods. Where portability was a prime concern, a Yellow Springs Instruments Telethermometer was used with a type 506 (22 gauge) hypodermic needle thermistor probe calibrated against a standard laboratory thermometer. Limpet temperatures were obtained by prying the animals off the rock, quickly inserting the needle probe into the center of the visceral mass, and immediately pressing the limpet onto its original location with a fingernail or pencil to minimize heat gain or loss. The maximum temperature indicated was recorded. This method required sacrificing a limpet for each temperature determination. Since body temperatures of limpets were virtually the same as temperatures of the adjacent rock surfaces (mean deviation of 12 specimens of *A. scabra* from rocks was $-0.33^{\circ}\text{C} \pm 0.19$ (S.E.) at 15:00, 8 August 1971), in many cases only rock surface temperatures were taken rather than depopulating the research area of limpets.

Where recordings of temperature fluctuations over an entire day were desired, a 12-channel Leeds-Northrup Speedomax thermocouple recorder was used, powered by a portable 115 V generator. Size 7 (#36 gauge) thermocouples were fastened to rock surfaces with lumps of modelling clay placed about 5 cm from the tip of the couple. Recordings of limpet body temperatures could also be obtained, without harm to the limpets, by slipping the tip of the thermocouple under the edge of the shell and fastening the leads down-as above.

Interspecific differences in maximum temperatures attained in the field were examined by selecting a study area in which all five species occurred, and recording the temperatures of the individuals of each species which appeared most exposed to solar radiation.

Windspeeds were measured with a Hastings-Raydist portable heated-thermocouple anemometer with an omnidirectional probe which allowed measurement of air movements 2 cm from the rock surface. Measurements were also taken at greater distances from the surface to permit comparison of microclimatic conditions with traditional macroclimatic readings.

Relative humidities were measured with a Hygrodynamics, Inc. electric hygrometer indicator. The probe was placed on the rock surface near the groups of limpets, shaded, and allowed to equilibrate with the air just above the surface. Humidity of air a meter above the surface was also measured.

Thermal tolerances of the five species were compared in the laboratory by a technique similar to that of Fraenkel (1968), which ensured that each individual received a similar heat dose. Tolerances in preliminary experiments were very consistent within species; small sample sizes were therefore used to both minimize cooling of the test bath by a large mass of cold limpets and to avoid needless destruction of animals. Six to ten limpets were allowed to adhere to the walls of a 500 ml beaker. The cold sea water in the beaker was then replaced with aerated sea water at the desired test temperature and the beaker placed in a water bath at the test temperature for 15 minutes. At the conclusion of the experiment the warm water was replaced with running sea water for recovery and assessment of survival. For each species the thermal lethal limit was defined as the lowest temperature killing more than half of the sample tested.

Survival at the conclusion of this and subsequent experiments was assessed after a 24-hour recovery period in running sea water. The criterion of survival was the resumption of normal locomotion, including the ability to adhere to and move about on an inverted glass surface. Animals incapable of normal locomotion, even if responsive to prodding or capable of some spontaneous movement, were considered "ecologically dead" since in the field they would undoubtedly be swept off the rock by surf and perish.

Most thermal tolerances were determined with limpets collected during the summer. Variation of these tolerances throughout the year, and in individuals from different intertidal heights, was checked by collecting *A. digitalis* and *A. scabra* from Zones I and II in winter and determining thermal tolerances during immersion as above.

To explore the relationship between thermal tolerances during immersion and those pertaining in the field, lethal limits were also determined in air with a slow temperature rise which would result in a heat dose equal to or greater than that which the limpets would experience in nature. Ten specimens of *A. digitalis*, *A. pelta*, or *A. scutum* were placed in each of several beakers and allowed to adhere to the walls as above. *Acmaca scabra* was omitted due to its poor fit to the smooth glass, and the consequent problem of desiccation; *A. persona* was omitted due to scarcity. The water was emptied out of the beakers and a few hours allowed for the surface to dry. The beakers were then placed in a recirculating wind tunnel with slow (0.5 m/sec) air movement, and the temperature of the limpets (monitored via thermocouples) was raised over a period of 5-6 hours to the lowest desired test temperature, as would naturally occur with limpets exposed by a morning tide. After 15 minutes at this temperature, the first sample of limpets was removed to be cooled and tested for survival. The temperature was raised 1° C and held for about 15 minutes, another sample removed, and so forth. Effect of size and desiccation state on thermal tolerance under these simulated natural conditions was assessed by including samples of very small and of moderately desiccated *A. digitalis*.

Determination of desiccation tolerances and rates required weighing, observa-

tion, or similar manipulations of limpets without disturbing them and causing adventitious water loss from the mantle cavity. These operations were carried out with the animals attached to discs of transparent 0.004 inch Mylar plastic film. Attachment was effected by immobilizing the limpets, shell downward, on lumps of modelling clay on a water table and presenting the disc to the foot. Healthy limpets attached securely to the disc and became quiescent after several hours or overnight on the water table.

Desiccation rates were always determined with moving air, since still air is not a natural situation. Furthermore, air movement is of such crucial importance to evaporation rates that the difference between truly still air and slight convection currents of unknown magnitude would introduce unacceptable uncertainty into measurements of desiccation rates. The use of moving air of constant velocity unfortunately precludes comparison with data of other workers who have used nominally still air (*e.g.*, Davies, 1969).

Progress of desiccation was followed by periodic weighings. Dry, shell and disc weights obtained after termination of the experiments allowed calculation of water lost at any time as a percentage of the initial gross weight, or as a percentage of the total initial body water (wet gross weight—dry gross weight). Because of variation in the shell component of gross weight, the latter figure is considered to be the most meaningful biologically and is the one used for most comparisons; the former allowed approximations where the animals could not be sacrificed for dry weights.

Desiccation rate studies in the laboratory were carried out in a closed, recirculating wind tunnel within a constant-temperature enclosure, with humidity controlled by pans of appropriate salt solutions (*Handbook of Chemistry and Physics*, Chemical Rubber Co., 1958).

Drying of limpets prior to determination of desiccation tolerances took place at 20° C and at 1.0–1.4 m/sec airflow. The humidity was that of the outside air drawn into the ventilating system (usually 50–80% R.H.). These conditions approximate those of a breezy, overcast day. Desiccation was begun after recording of initial weights. Then, several times each day, those animals which appeared near death were removed, weighed again, and checked for survival; dry weights were subsequently obtained. The lowest desiccation levels causing 50% or higher mortality in samples of each species were designated the desiccation tolerance limits.

Tolerance of *A. t. scutum* was also determined under less severe drying conditions to check the effects of rate of desiccation on desiccation tolerance.

Survival at the conclusion of these experiments was assessed as described above.

Since initial hydrated weights of limpets in the field were not available, the weighing method could not be used for field measurements of desiccation. Therefore, a graph was prepared from laboratory data comparing water loss, measured gravimetrically, with chloride concentration in mantle-cavity water/urine (“extra-corporeal water”) of 78 specimens of *A. digitalis*. The chloride determinations were carried out on 1 microliter samples of fluid with a Buchler-Cotlove Chloridometer. The resulting curve (Fig. 1) was used to translate chloride concentrations of extra-corporeal water obtained from animals in the field into per cent body water lost at the time the sample was collected.

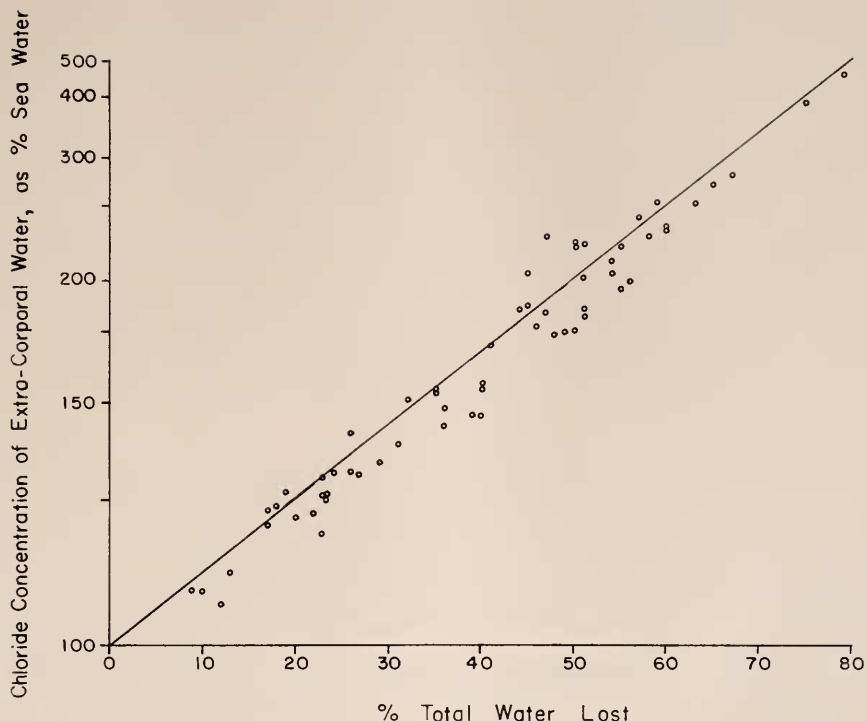


FIGURE 1. Evaporative concentration during desiccation in *Acmaea digitalis*. Line represents values calculated for evaporation of water from an ideal salt solution. To linearize data, vertical scale is proportional to $1 - (100/\text{concentration})$.

Equilibration rates and tolerances to fresh water were determined by allowing groups of limpets to attach to plastic film as described above, immersing them in fresh water at 15°C , and sampling the population at intervals. Since flow rates profoundly influence boundary layers and diffusion rates, still water was used to provide identical, although somewhat unnatural, conditions for all limpets. Animals removed from the fresh water were allowed about two hours in still air to equilibrate body fluids with the mantle cavity water and urine ("extra-corporal water" or E.C.W.). The "extra-corporal water" was sampled via a capillary micropipette after removing the limpet from the substrate, and if necessary, gently pressing the foot. No distinction was made between mantle-cavity fluid and urine because there appears to be no osmoregulation between them (Webber and Dehnel, 1968). Chloride concentration was determined with a Buchler-Cotlove chloridometer. The animals were subsequently assessed for survival.

Comparison of concentrations of blood and E.C.W. in freshwater stressed animals was made both with the Chloridometer and with a nanoliter freezing-point osmometer (Clifton Technical Physics). Blood samples were obtained after all extra-corporal water had been expressed and blotted away. The foot was slit and the blood that seeped into the cut was then drawn up in a capillary micropipette.

Pressure on the foot usually aided this process. Samples for osmometry were kept deep-frozen under oil until processed. For ease of comparison, all concentrations are expressed as per cent sea water, where 100% sea water has a salinity of 35‰.

Tolerance to acute immersion in solutions hyperosmotic to sea water was tested by immersing limpets for 5 hours in aerated solutions, followed by return to running sea water for subsequent assessment of survival. Test solutions were made up from sea water and stock 500%–700% sea water prepared by boiling under vacuum, or with "Seven Seas Marine Mix" (Utility Chemical Company).

The effects of a gradual rise of salinity were examined by gradually adding concentrated sea water to a small quantity of normal sea water containing the experimental animals. Aeration and mixing were effected by bubbling from airstones. Periodically the salinity of the bath was determined with a Goldberg refractometer (American Optical), and samples of the limpet population were removed and placed in running sea water to check for recovery.

Rate of equilibration of limpets to 500% sea water was determined by suspending four specimens of *A. digitalis* by a fine wire from the pan hook of an analytic balance. A beaker of the hyperosmotic solution was raised to cover the limpets, and their weight while immersed was recorded at intervals for 24 hours. Weight while immersed is equal to limpet volume multiplied by (limpet density—solution density), where solution density may be considered constant. Either osmotic loss of water from the limpets, which decreases limpet volume and increases limpet density, or osmotic uptake of salts by the limpets, which increases limpet density, will cause an increase in weight while immersed. Thus this technique permits measurement of osmotic equilibration occurring through either salt or water movements, or both.

The degree of volume regulation, or of osmotic dehydration, was checked by immersing *Acmaea digitalis* on plastic sheets overnight in 400% sea water and comparing loss in wet blotted weight with initial total water (initial wet blotted weight minus dry weight with shell).

Fresh water dilution or evaporative concentration of limpets in the field was measured by drawing 1 microliter samples of E.C.W. into capillary micropipettes from limpets freshly removed from the rock surface. The samples were stored in the capillaries under oil until their concentration was determined with the Chloridometer.

RESULTS

Air, rock surface, and limpet temperatures fluctuated similarly in both Zones I and II. Nighttime temperatures reached a minimum between 03:00 and 06:00. On a few occasions, mild frosts (-2° C) occurred during the winter, but limpet temperatures never dropped below freezing. In the morning, temperatures rose until the sun was past its zenith, then fell gradually until the returning tide caused an abrupt drop to sea surface temperature. The highest temperatures of rock surfaces and individual limpets were recorded on clear, calm, sunny days (Table I) when the lower low tide occurred during the late morning and left much of the intertidal exposed during the hottest part of the day.

The temperatures of limpets and the rock surfaces adjacent to their roosting



TABLE I

Climatic conditions and maximum temperatures of air, rock surfaces, and limpets on Bodega head

Date (13:00-15:00 Pacific Standard Time)	Weather	Air, °C		Rock surface °C	<i>A. scabra</i> °C	Wind, m/sec	
		2 m	1 cm			2 m	1 cm
26 Sept. 70	Sunny, calm, hot	22.5	26	37	37	1.8	0.5
31 May 70	Sunny, calm, hot	22.5	—	38	38	1.8	0.5
Undated, 1968	Sunny, calm, hot	—	—	41	41	—	—
5 Aug. 70	Clear, cool, windy	16	20	27	28	2.7-3.6	1.4-1.8
13 Aug. 70	Intermittent fog, cool, windy						
	Zone I	15	21	26	26	1.8-2.3	0.9
	Zone II	15	22	26	25	1.8-2.3	0.9

sites depended primarily on their orientation to the sun, and to wind and spray. Intertidal height was of secondary importance, serving principally to determine the length of exposure to high temperatures. Since Zone II is exposed for shorter periods, the probability of tidal exposure coinciding with the hottest part of the day is lower than in Zone I, and maximum temperatures usually were lower in Zone II. However, on occasions when both Zone I and Zone II were exposed during the heat of the day, maximum temperatures of sites similarly exposed to the sun could be virtually identical in both zones (Table I).

Nevertheless, in a given area containing all five species, the maximum temperatures of those individual limpets most exposed to solar radiation showed pronounced interspecific differences. Maximum temperatures of *A. scabra* were higher than those of the most exposed *A. digitalis*, which in turn were higher than those of *A. persona*, *A. pelta* and *A. t. scutum* in the same area (Table II).

TABLE II

Field temperatures of individual limpets most exposed to sun, °C.

	Max.	Mean	Min.	(n)
25 March 1969 15:00				
<i>A. digitalis</i>	30	30	26	10
<i>A. scabra</i>	37	32	28	9
18 May 1971 14:00-15:00				
<i>A. digitalis</i>	29.5	28	26	5
<i>A. scabra</i>	34	34	33	3
<i>A. persona</i>	20	20	19	5
<i>A. pelta</i>	27	23	19	14
<i>A. scutum</i>	27	24	20	11

TABLE III

Thermal tolerances while immersed. Boldface denotes thermal lethal limits; sample n = 6

Test temperature °C	% Mortality				
	<i>A. pelta</i>	<i>A. scutum</i>	<i>A. persona</i>	<i>A. digitalis</i>	<i>A. scabra</i>
33-34	0				
34-35	50	0	0		
35-36	100	100	20		
36-37	100	100	20		
37-38	100	100	80	0	0
38-39			100	83	17
39-40			100	100	0
40-41				100	67
41-42				100	100

Thermal tolerances of the five species, determined during immersion in sea water, are lower for the Zone II species, intermediate for *A. persona*, and higher for the remaining Zone I species (Table III). Tolerances of *A. scabra* and *A. digitalis*, which experience the widest range of microclimates, were essentially constant regardless of season or collecting site: those of winter-collected samples were at most 1° C below those of summer samples; those of *A. scabra* and *A. digitalis* collected in Zone II were at most 1° C below those of Zone I samples. Thus, there appears to be little acclimation of thermal tolerances.

Thermal tolerances determined under simulated natural conditions were about 5° C higher than tolerances determined during immersion (Table III) for *A. digitalis*, *A. pelta*, and *A. t. scutum*, and presumably for the remaining species as well. Thermal tolerance seems to be independent of size; no differences were evident between small (9.0 ± 0.27 mm) and large specimens of (16.4 ± 0.28 mm) *A. digitalis*. However, removal of 20% to 60% of the total body water by desiccation did reduce the thermal tolerance of *A. digitalis* by about 3° C.

Both the usual and extreme values of the factors pertinent to desiccation—temperature, humidity (as vapor pressure deficit), and windspeed—are summarized in Table IV. Figures for usual conditions are estimates from measure-

TABLE IV

Typical and extreme environmental conditions

Weather type	Windspeed m/sec.		Temperature, °C			Vapor pressure deficit mm Hg	
	2 m above surface	2 cm above surface	1 m above surface	1 cm above surface	Surface	1 m above surface	2 cm above surface
Foggy	0-2.2	0-1	8.5-15	15-21	15-27	1-2	1-4
Clear, cold, windy	4.5-13.5	2.2-4.5	6.5-10		15-27	4-5	
Clear, warm, windless (extreme)	0-2.2	0-1	21	27-33	38-41	12-15	23-30

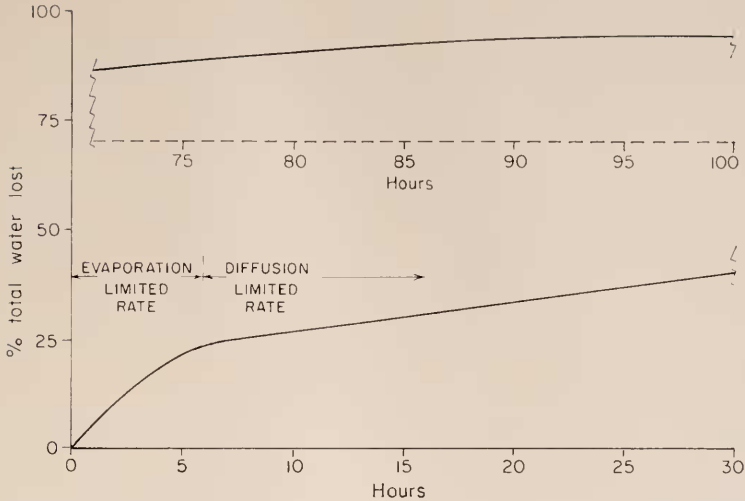


FIGURE 2. Desiccation of permeable bodies under constant conditions: typical time course.

ments taken on "typical" days, while extremes are maximum measurements obtained during several periods of hot weather occurring in 1968–1971. These data were used to determine realistic conditions for desiccation rate and tolerance experiments in the laboratory, and in interpretation of the results.

Desiccation rates of all five species of limpets, living or dead, or limpet shells filled with 15% gelatin, or even small glass vials filled with 15% gelatin, showed a pattern similar to Figure 2 under constant conditions. A high initial rate of water loss, which after a time declines to a lower, fairly constant rate, is characteristic of water-containing permeable bodies exposed to constant drying conditions. The initial rapid loss occurs during the period when evaporation of free water from the surface is the rate-limiting factor; for a given surface this rate is a function of environmental conditions. The subsequent lower rate of water loss represents that portion of desiccation in which free water has disappeared and the rate-limiting factor is the supply of water to the evaporating surface from the underlying matrix. This rate depends on internal diffusion coefficients, which are characteristic of the permeable body. The initial rapid loss rates were highly variable within species of limpets; hence, the diffusion limited portion of the curve, being considered more characteristic of the animals, was used for all comparisons.

All of the species showed a lifting of the shell at high temperatures, cited by Segal and Dehnel (1962) as a mechanism for evaporative cooling. However, this occurred only in water or near-saturated air and was abolished by application of even mild drying conditions. Under desiccating conditions the limpets tend to conserve water rather than using it to regulate body temperature; the shell-lifting response is probably evidence of impending heat coma.

Average desiccation rates under conditions approximating a cool windy day at Bodega Head, using 25–30 individuals of each species, were markedly lower in the Zone I limpets than in the Zone II species (Table V). *Acmaea scabra* was

TABLE V

Desiccation rates under constant conditions; % total water lost/hr; mean \pm S.E. ($n = 25-30$); at 18°C: Zone I rates < Zone II rates, $P < 0.05$; differences within zones not significant ($P > 0.05$); at 30°C: *A. pelta* rate < *A. t. scutum* rate, $P < 0.05$; all other differences, $P < 0.001$

	1.4 m/sec 7 mm Hg VPD* 18°C	1.4 m/sec 30 mm Hg VPD* 30°C	2.8 m/sec 30 mm Hg VPD* 30°C
<i>A. digitalis</i>	0.32 \pm 0.02	0.66 \pm 0.05	1.02 \pm 0.11
<i>A. persona</i>	0.28 \pm 0.02	3.26 \pm 0.18	—
<i>A. pelta</i>	1.02 \pm 0.14	5.56 \pm 0.28	—
<i>A. t. scutum</i>	1.29 \pm 0.10	7.26 \pm 0.68	—

* VPD = vapor pressure deficit.

omitted since the serrated shell margins of this species would not fit closely to the plastic discs, as they would to the rock.

Under more rigorous conditions, simulating those occurring during unusually warm weather, all four species tested lost water at higher rates. The increase of rate in the Zone II species was roughly proportional to the increase in vapor pressure deficit, as expected from the general evaporation formula:

$$\text{Evaporation} = K (\text{vapor pressure deficit}) C \left(\frac{\text{windspeed}}{\text{length of evaporating surface}} \right)^n$$

(Leighly, 1937). However, the rate increase in *A. digitalis* was only half of what would be predicted on the basis of the formula, implying the existence of some sort of regulation of water loss, as demonstrated by Machin (1965) in his elegant series of papers on desiccation of *Helix*. The increase in desiccation rate of *A. persona* is nearly three times that predicted by the evaporation formula, possibly implying the breakdown of a regulatory mechanism at an elevated temperature not usually experienced by this shade-dwelling limpet. Doubling the windspeed increased the desiccation rate of *A. digitalis* by a factor of 1.5, suggesting that the exponent "n" in Leighly's formula is about 0.5, i.e., that desiccation rate of limpets is roughly proportional to the square root of windspeed (Table V). Desiccation continues even when conditions during exposure do not appear at all stressful; 20 specimens of *Acmaea digitalis*, pre-dried until 20 to 75% total water had been lost, and then exposed outside overnight in fog, continued to lose water (a maximum of 5% total water lost overnight).

Two characteristics of limpets appeared at the outset particularly likely to affect desiccation rates: size and shell circumference. During the course of the study a third factor became evident: an ability of the Zone I limpets to form a mucus sheet between the shell margin and the rock surface.

Intraspecifically, no clear relationship was evident between size and desiccation rates in the laboratory. However, increased body size apparently does result in reduced desiccation rate and mortality in the field, as is indicated by the extracorporeal water concentrations and mortality in three size classes of *A. scabra* collected late in the afternoon after a full day of exposure to warm dry weather

TABLE VI

Chloride concentration in extra-corporeal water and survival of field-desiccated Acmaea scabra

Size group mm	Chloride concentration of E.C.W. (% sea water)		Survival	
	$\bar{x} \pm \text{S.E.}$	n_1^*	%	n_2^*
7-12.9	438 \pm 23.2	13	31	29
13-16	356 \pm 22.1	10	55	11
17-24	303 \pm 22.2	18	63	19

* Difference between n_1 and n_2 is number of individuals from which no fluid was obtainable (internal concentration presumed above 500% sea water).

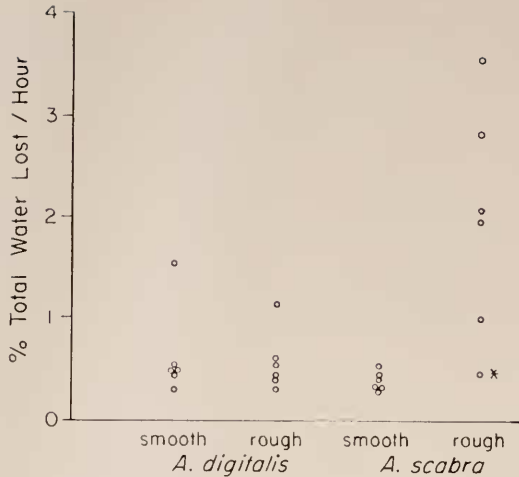
(Table VI). Interspecifically, the relationships expected on the basis of surface: volume ratios were not observed; the larger species, *Acmaea pelta* and *A. t. scutum*, lost water at higher rates than did the smaller *A. digitalis* and *A. scabra* (Table V).

Since virtually all evaporative water loss occurs through the gap between the shell and the substrate, the relative circumferences in several sets of shells of equal volumes were measured. *Acmaea scabra* was omitted due to the difficulty of estimating circumference and volume, caused by the serrated shell margin. Flat-shelled *A. t. scutum* had the greatest relative circumference, which was at most 25% greater than that of *A. digitalis*, a minor difference compared to the observed differences in desiccation rates.

The third factor of possible significance in determining desiccation rates, the ability of *A. digitalis*, *A. persona*, and to a lesser extent, *A. scabra*, to form a sheet of mucus between the margin of the shell and the substrate (Fig. 3), was noticed during preliminary desiccation experiments and was subsequently found to be a regular occurrence. The sheet is produced by extension of the mantle until it contacts the substrate, secretion of a layer of viscid mucus on the entire exposed



FIGURE 3. *Acmaea digitalis* on rough granite, with mucous diffusion barrier spanning gaps between the shell margin and the uneven substrate.



* Formed complete mucus sheet

FIGURE 4. Desiccation rates: effect of shell fit to substrate. "Smooth" shells fit substrate closely; "rough" shells fit substrate poorly.

area of the mantle, and subsequent withdrawal of the mantle. The mucus remains in place and gradually dries as the animal within desiccates. Individuals of *A. digitalis* and *A. persona* regularly spanned gaps of up to 15% of the shell diameter; *A. scabra* apparently has a much more limited ability to produce the mucus sheet and usually could not span gaps of this magnitude without leaving perforations in the sheet.

To assess the importance of this mucus sheet in slowing desiccation, desiccation rates of *A. digitalis* with the normal smooth shell margins, *A. digitalis* with chipped shell margins, *A. scabra* with smooth shell margins from the artificial tide system, and *A. scabra* with the normal rough shell margins were compared. All of these animals were desiccated on smooth mylar discs: those with smooth margins fitted the substrate well, while those with chipped or rough margins had gaps between shell and substrate. The smooth-margin *A. digitalis*, rough-margin *A. digitalis*, and smooth-margin *A. scabra* all exhibited about the same rate of water-loss, while the rough-margin *A. scabra* had an average desiccation rate approximately five times higher (Fig. 4). An exception to this was the individual noted by an asterisk, which was the only rough-margin *A. scabra* observed to form a complete mucus sheet. This individual showed a desiccation rate similar to those of the other groups. These results indicate that the normal desiccation rate of *A. scabra* on its homesite is about the same as that of *A. digitalis* which does not home.

The effect of removing the mucus sheet was investigated with four groups of *A. digitalis*. Two of these had the normal smooth shell margins and fitted the Mylar discs well; the other two groups had the shell margins chipped and consequently fitted the discs poorly. Progress of desiccation was followed by periodic

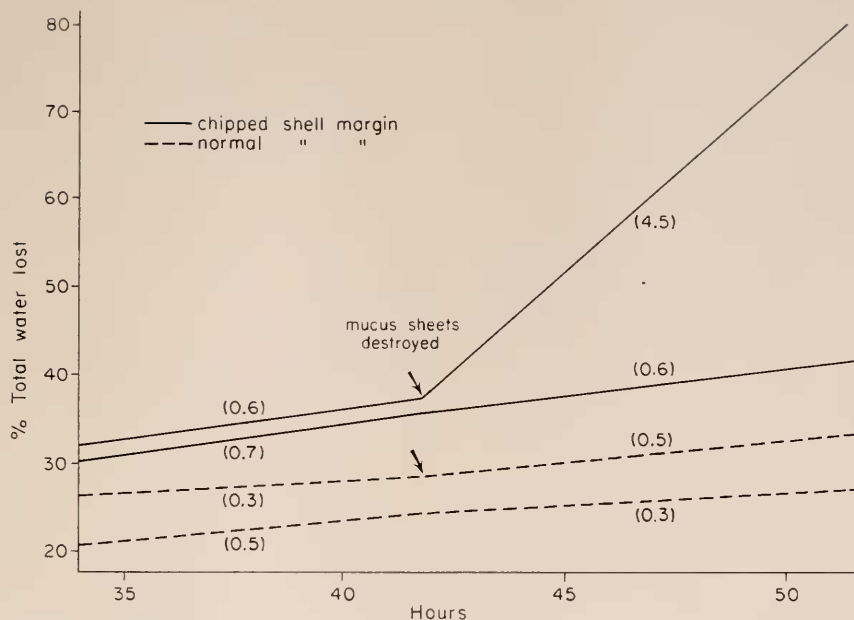


FIGURE 5. Desiccation rate: effect of removing mucus sheet (*Acmaea digitalis*). Lines drawn through points not on graph; 30° C; 30 mm Hg vapor pressure deficit; 1.0 m/sec air flow. Slopes indicated as % total water lost/hour.

weighings, and the mucus sheets of one smooth and one rough group were destroyed after every other weighing. *Acmaea digitalis* regularly repaired the mucus sheet until over 35% of their total water had been lost. Permanently obliterating

TABLE VII

Desiccation tolerances (number surviving/number in interval); 20°C; windspeed 1.0-1.4 m/sec. Boldface denotes interval of 50% mortality (desiccation lethal limit)

% water lost	<i>A. digitalis</i>	<i>A. scabra</i>	<i>A. persona</i>	<i>A. pella</i>	<i>A. scutum</i>	Equivalent osmotic concentration (% sea water)
60-62	2/2	2/2	0/0	0/0	3/3	250-263
62-64	1/1	3/1	2/2	0/0	2/3	263-278
64-66	0/0	2/2	1/1	1/1	2/4	278-294
66-68	1/1	3/3	1/1	0/0	2/5	294-312
68-70	1/1	3/3	2/3	2/2	4/7	312-333
70-72	0/0	2/2	0/1	0/0	3/7	333-357
72-74	2/2	2/3	2/2	3/5	1/3	357-385
74-76	1/1	3/3	2/2	0/0	1/6	385-416
76-78	0/0	1/1	2/2	0/2	0/1	416-455
78-80	0/0	0/1	0/1	0/3	0/4	455-500
80-82	3/5	1/3	1/4	0/2	0/1	500-555
82-84	0/1	0/0	1/3	0/1	0/0	555-625
84-86	0/2	0/1	1/2	0/1	0/0	625-715
86-88	0/5	0/5	0/2	0/0	0/0	715-833

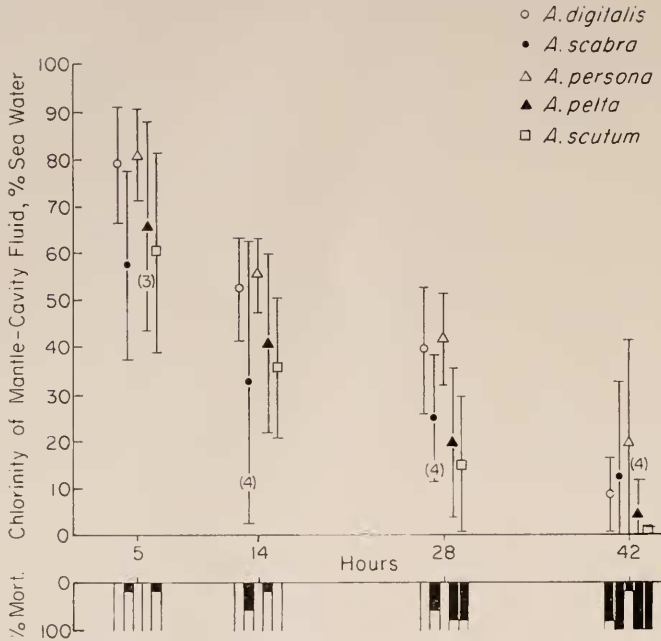


FIGURE 6. Dilution and mortality of limpets during immersion in fresh water. Sample size equals 5 unless otherwise indicated by numbers in parentheses.

the mucus sheet of a representative rough-margin individual of *A. digitalis* caused a seven-fold increase in desiccation rate, while the rates of a representative smooth-margin individual (which repaired the sheet), and of undisturbed rough- and smooth-margin individuals, remained essentially unchanged (Fig. 5).

Desiccation tolerances of the five species of limpets under conditions approximating a cool, breezy day (20°C , 1–1.4 m/sec wind), expressed as per cent of total body water lost and as corresponding internal osmotic concentrations (Table VII), are correlated with the intertidal height of each species' normal habitat.

Acmaea testudinalis scutum, a Zone II limpet, was also desiccated under less severe conditions, which caused it to lose water at a rate similar to that shown by the Zone I limpets under the above conditions. Groups were removed and tested for survival during the second and third days of the experiment. These groups experienced 100% mortality, although many individuals had lost less than 65% of their total body water, indicating that tolerance to desiccation decreases with increasing length of exposure to drying conditions.

To examine the implications of rainwater runoff, all five species of limpets were exposed to standing fresh water for 4, 14, 28, and 42 hours. Chloride concentration of extra-corporeal water (E.C.W.) and survival in each group are plotted in Figure 6. *Acmaea digitalis* and *A. persona* survived somewhat longer than the other species, although no significant differences in equilibration rate are apparent. Longer survival may be the result of slightly greater tolerances to dilution in these

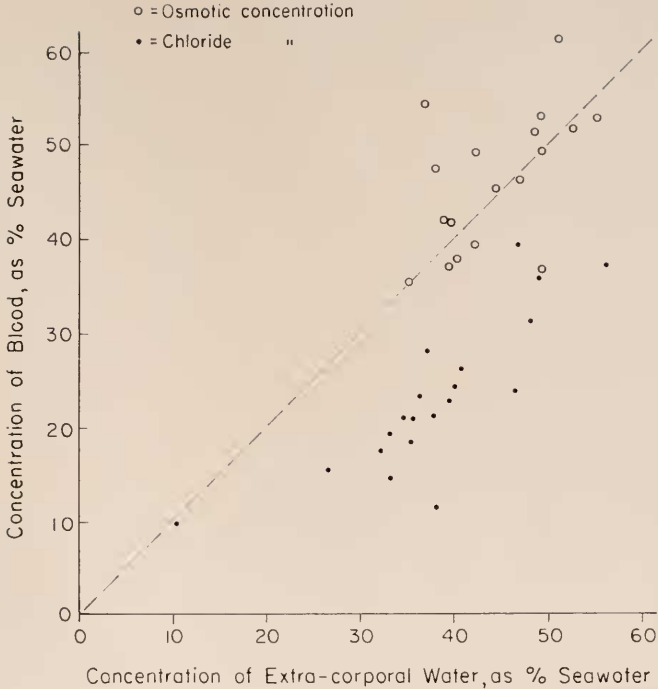


FIGURE 7. Concentration of blood and extra-corporeal water in fresh water stressed *Acmaea digitalis*.

two species. Precise determinations of dilution tolerances were not made since it is impossible to estimate visually when the animals are near death, and excessive numbers of animals would have to be sacrificed to accumulate sufficient data to define the lethal limit. Extra-corporeal water concentrations at which limpets died (Fig. 6) indicate that the limit for all five species is around 30% sea water.

Dilution of E.C.W. caused a decline in blood chloride concentrations to values below those of the E.C.W. However, total osmotic pressure of E.C.W. and blood was found to be the same (Fig. 7), indicating that much of the remaining blood osmotic pressure is due to non-ionic solutes, which osmotically balance the excess salts in the E.C.W.

Fresh-water seepage following rainstorms does leach salts out of limpets in the field. A single tidal exposure in a seep of 1.7% sea water depressed E.C.W. chloride in 5 individuals of *A. digitalis* to 38-40% sea water—near the lethal limit. Presumably extending exposure by another day would have caused death.

The osmotic effects of evaporative water loss were investigated by comparing weight loss and chloride concentration of E.C.W. in laboratory-desiccated animals (Fig. 1). The line represents data calculated for evaporation from an ideal salt solution; the fit of experimental limpet data to this line indicates that salts are being neither voided into the mantle cavity water and urine compartments, nor sequestered in the body during the progress of desiccation. Internal osmotic concentra-

TABLE VIII

Water content of five species of *Acmaea*, including two size classes of *A. scabra*

Species	% Water in total hydrated weight of soft parts (mean \pm S.E.)
<i>A. digitalis</i>	85.81 \pm 0.24 (n = 62)
<i>A. scabra</i>	86.81 \pm 0.27 (n = 68)
0.3-0.8 g	87.00 \pm 0.38 (n = 9)
1.4-2.4 g	86.90 \pm 1.09 (n = 11)
<i>A. persona</i>	85.88 \pm 0.29 (n = 24)
<i>A. pelta</i>	88.73 \pm 0.32 (n = 36)
<i>A. scutum</i>	87.33 \pm 0.48 (n = 25)
<i>A. digitalis</i>	
<i>A. pelta</i> > <i>A. scabra</i> ($P < 0.05$)	
<i>A. persona</i>	
<i>A. scutum</i> > <i>A. digitalis</i> ($P < 0.05$)	
All other differences not significant at 5% level.	

tions expected in animals of each species at their respective lethal limits of desiccation (Table VII) were obtained from Figure 1.

Chloride concentrations of E.C.W., where fluid was still obtainable, and survival of three size groups of *A. scabra* collected after a warm dry day are shown in Table VI. Concentrations in the smallest group are significantly ($P < 0.05$) higher than in the largest group, as is the proportion of animals with no obtainable fluid (chloride concentration presumed above 500% sea water). Survival increases with increasing size.

Water content of fully hydrated limpets established on Mylar discs

(Total Water, Hydrated/Weight of Soft Parts, Hydrated)

was similar for all five species and for both large and small *A. scabra* (Table VIII).

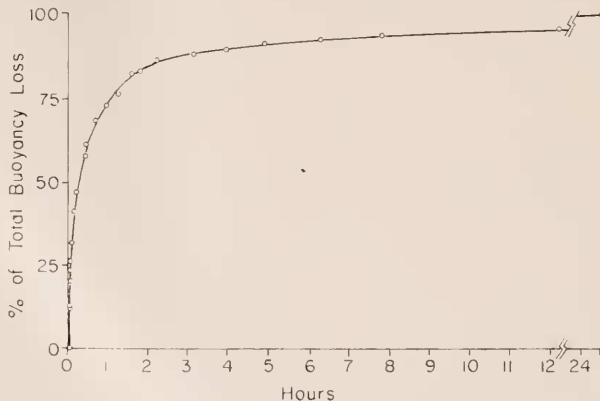


FIGURE 8. Equilibration of *Acmaea digitalis* to 500% sea water, as shown by buoyancy changes.

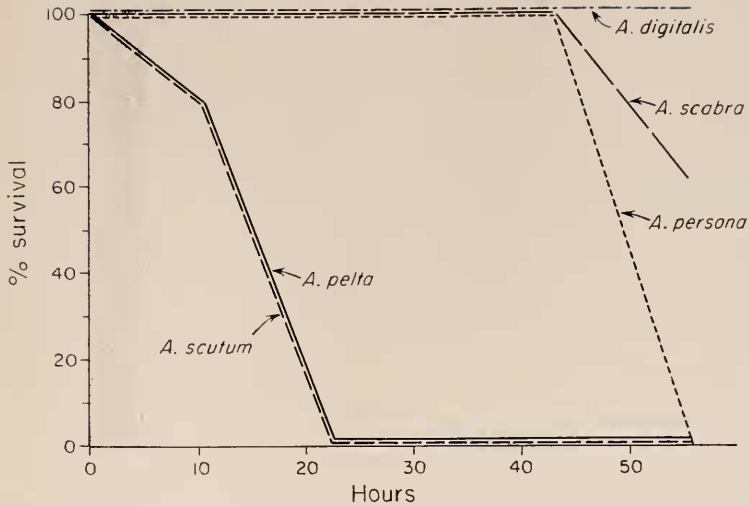


FIGURE 9. Survival in 400‰ sea water. Concentration raised from 100‰ to 400‰ sea water during first 5 hours (stippled area).

All five species tolerated 5-hour immersion in concentrations up to 400‰ sea water; at 500 and 600‰ sea water the majority of *A. pelta* and *A. scutum* perished while the majority of the Zone I limpets survived. Equilibration of *A. digitalis* to 500‰ sea water, as shown by changes in weight while immersed due to water loss and salt uptake, was 90% complete in 4 hours (Fig. 8).

Under more natural conditions of gradual salinity rise, the Zone I limpets tolerated 400‰ sea water longer than the other species (Fig. 9). The osmotic stress produced by immersion in 400‰ sea water is equivalent to that produced by evaporative loss of 75% of the total water. However, since limpets perform limited volume regulation, osmotic dehydration in 400‰ sea water removes only $28\% \pm 5\%$ (mean \pm S.E.; $n = 10$ *A. digitalis*) of the total water. Thus the effect of the same osmotic stress produced by prolonged desiccation can be examined in the absence of excessive tissue dehydration.

Gradually raising salinity over 20 hours to 250‰ sea water simulated the osmotic effect of evaporatively removing 60% of the total water, a level well below the acute tolerances of even *A. pelta* and *A. t. scutum*. Nevertheless, both *A. pelta* and *A. t. scutum* began to die early in the second day of exposure and all were dead within 33 hours.

DISCUSSION

Are range limits of animal populations determined by physiological tolerances to abiotic environmental factors, or does some biotic factor—*e.g.*, behavior or competition—prevent occupation of the entire physiologically acceptable range? The intertidal zone is an obvious habitat in which to explore this question, since it represents one of the sharpest gradients in physical conditions to be found on this planet. The marine grades into the terrestrial environment over the space

of a few meters, and animals invading this zone from the sea encounter progressively greater physiological challenges. Obviously, these animals cannot survive above some critical level in the intertidal, determined by the extent of their dependence on sea water. In this sense their ranges are potentially limited by the intolerable conditions prevailing above that level. However, it remains to be demonstrated that they do live everywhere that physical conditions are tolerable, and that partitioning of the intertidal gradient is thus determined principally by interspecific differences in physiological tolerances.

The acmaeid limpets present a convenient system in which to approach this problem, because there are several abundant species which collectively occupy the entire intertidal range. Like the barnacles, they are abundant and easily accessible, but have the additional advantage of being removable, allowing manipulative and laboratory experiments. Adult limpets live several years (Frank, 1965a; Sutherland, 1970) and are thus exposed to the climatic extremes occurring in all seasons. The response of all of these limpets to tidal exposure is immobility—the “clamp-down response” of McAlister and Fisher (1968). The animals are thus behaviorally trapped and must endure any stressful conditions until the tide returns. The aquatic microenvironment of such “roosting” limpets is the small quantity of water retained under the shell. Due to its minute volume, the thermal, evaporative, and osmotic effects of exposure are far more rapid and dramatic than would be the case in organisms protected by the larger water mass of tidepools.

The physical environmental factors representing potential stresses to limpets differ according to season. During the winter, both rainwater runoff during storms and seepage of freshwater from the cliffs present potential osmotic problems. Limpets appear to have no defense, other than the “clamp-down response,” against dilution by fresh water. Like most other gastropods, they are osmoconformers. Fluctuations in the osmotic concentration of mantle-cavity fluid from 23% to 150% sea water are closely paralleled by fluctuations in concentration of the three major internal fluid compartments (urine, blood, and intracellular fluid) in *Acmaea limatula* (Segal and Dehnel, 1962), from 50% to 125% sea water in *A. t. scutum* (Webber and Dehnel, 1968). Blood of *A. digitalis* is in osmotic equilibrium with diluted extra-corporeal water (mantle-cavity water and urine); blood chloride levels are even lower than those of the extra-corporeal water, presumably due to the presence of osmotically active organic compounds in the blood (Fig. 7).

Despite their apparent vulnerability to dilution by fresh water trickling down the rock surface, the various species of *Acmaea* show no pronounced differences in either resistance to dilution or tolerance of depressed internal electrolyte concentrations (Fig. 6), suggesting that no strong differential selection for these traits is taking place in the field. This seems to be true in the vast majority of the rocky intertidal at Bodega Head. Rainfall usually comes during storms, which bring high winds and rough seas. The effective tidal level is elevated by the resulting splash and salt spray. Consequently, the actual maximum period of vulnerability to rainwater runoff is shorter than the tidal exposure predicted on the basis of calm sea conditions. It is therefore unlikely to exceed 24 hours in Zone I, and must be less than 19 hours in Zone II (Sutherland, 1970). All of the species tested, with the exception of *A. scabra*, are able to withstand immersion in fresh

water for longer than the maximum expected exposure in their natural habitat (Fig. 6). (*A. scabra* was prevented by its very irregular shell margin from effectively clamping down on the flat plastic substratum during immersion in the laboratory, and consequently lost salts at a disproportionately high rate. The close fit of shell to rock would presumably abolish this effect in the field.) Furthermore, since rain at Bodega Head generally falls in a series of brief showers, it is improbable that rain would fall continuously for even 19 hours coinciding with a period of tidal exposure. Thus lethal, or even stressful, dilution by winter rainfall appears to be an extremely unlikely situation for even the highest of the limpets.

An exception occurs in areas which form fresh-water seeps during the winter and spring months. Many of these areas are located in embayments in the cliffs and support a heavy film of algae, representing a rich food resource. Due to their geometry they are kept wet with salt spray when storm surf is running. During winter storms *A. digitalis* normally moves upward, then moves down in summer (Frank, 1965a; Miller, 1968); at Bodega it seems to move upward into the seep areas under the protection of the storm-wave spray. When a storm brings a large amount of rain and is followed by calm weather and low seas, the result is both an augmentation of the seepage rate and a drastic reduction or cessation of salt-spray falling on seep areas. Limpets which have moved into the path of the seeping fresh water risk becoming trapped by their clamp-down response and suffering fatal dilution unless subsequent tides bring sufficient salt-spray to enable them to move out of the area. There may be small interspecific differences in adaptation to these conditions; the slightly longer survival of *A. digitalis* and *A. persona* in fresh water (Fig. 6) is correlated with the observation that only these species move into the seep areas. It is also possible that lethal dilution occurs, limiting further exploitation of seep areas: in a seep area the day after a storm (19 January 1970), extra-corporeal water concentrations of *A. digitalis* were as low as 38% sea water, and subsequently all limpets disappeared from the area. The data are not conclusive but suggest that the penetration of seeps and the extent of their utilization by Zone I limpets are limited by physical factors.

During the spring and summer, virtually no rain falls on Bodega Head, and the potential limiting factors are solar heating and desiccation. Adaptive interspecific differences in temperature tolerance do exist. Thermal lethal limits during immersion are correlated with the microhabitats in which the various species are normally found (Table III), as is the case in many groups of intertidal animals (Gowanloch and Hayes, 1926; Evans, 1948; Gunter, 1957). The highest tolerance is shown by *A. scabra*, which occupies primarily horizontal surfaces in Zone I, often directly exposed to the full force of the sun's rays (Haven, 1970) and which is limited in mobility by its homing habit. *Acmaea digitalis* has a somewhat lower tolerance; it generally occupies more vertical or overhanging surfaces in Zone I (Haven, 1970) which are shaded during much of the day. *Acmaea persona*, the third Zone I species, shows strong negative phototaxis, spending daylight hours chiefly in dark crannies or under boulders; it has a lower tolerance yet. The Zone II limpets, *A. pelta* and *A. t. scutum*, are characteristically found on the walls of shady surge channels or in the shelter of macroscopic algae (e.g., *Porphyra*, *Pelvetiopsis*, *Endocladia*) and are seldom exposed long enough to experience

extreme solar heating. They have the lowest temperature tolerances of the five species tested.

These thermal tolerances show little or no seasonal acclimation. This, although in contrast to the situation reported for lethal limits of some intertidal molluscs on English shores (Newell, Pye, and Ahsanullah, 1971), is not surprising. Limpets would be expected to show acclimation responses to regular, predictably changing environmental variables, such as sea water temperatures, and not to transient, unpredictable stimuli such as sudden periods of high temperatures during tidal exposure. In England, rising sea water temperatures precede the spring and summer, when thermal stress during exposure is likely; thus they serve as a cue for compensatory acclimation. On the other hand, spring and summer on the California coast are preceded by minimum sea water temperatures (Sutherland, 1970). Thus, although other functions in *Acmaca* have been shown to acclimate seasonally (*e.g.*, heart rate; Segal, 1956b), any compensatory acclimation of thermal lethal limits in response to changes in sea water temperature would be non-adaptive. In the absence of acclimation, the lack of intraspecific variation in thermal tolerance among individuals collected from different zones or microhabitats is to be expected. The free spawning habits and pelagic larvae of limpets ensure thorough mixing of gametes from all tidal levels, and preclude the local formation of physiologically different races.

The existence of interspecific differences in thermal tolerance, correlated with distributions, supports the hypothesis that high temperatures serve as a limiting factor in limpet zonation. However, the second criterion necessary to establish the hypothesis is not fulfilled. Rock surface temperatures never exceeded the lethal limits (as determined under simulated natural conditions) of even *A. pelta* and *A. t. scutum*, the most susceptible species tested. The observed differences in physiological adaptations to high temperatures are probably concerned with adjustment of optimal temperature ranges and with coping with extended sublethal thermal stresses, rather than with extension of lethal limits. On the basis of thermal lethal limits alone, any of the species could theoretically live anywhere in the Bodega Head intertidal.

In actuality, none of the species is found throughout the entire intertidal zone; each is found in a characteristic thermal microclimate. The highest limpet temperatures were observed in *A. scabra* which had homesites on rock surfaces perpendicular to the sun's rays. Similar temperatures certainly occurred at similarly exposed sites available to other limpets elsewhere in Zone I, and probably in Zone II. However, diligent search revealed that *A. digitalis*, *A. persona*, *A. pelta*, and *A. t. scutum* invariably occupied microsites which were shaded most of the day or received only oblique sunlight—never those directly exposed to the sun. These roosting sites were always several degrees cooler than the more horizontal, sun-baked sites occupied by maximally exposed *A. scabra* (Table II). They were never observed to approach lethal temperatures of the occupants, even assuming lethal limits to have been depressed several degrees by desiccation. Although non-homing limpets often shift their roosting sites (Frank, 1964), they are never found in "hot spots." This suggests that the observed distribution is due to behavioral selection of "safe" microsites by these species, as in Zone I *Littorina* (Bock and Johnson, 1967), rather than to elimination of less tolerant limpets

which wander into exposed locations. *A. scabra* is unique among the species examined, in that many individuals are restricted to the potentially most stressful areas of the intertidal by their homing habit and resultant low mobility.

No temperatures above the lethal limit of *A. scabra* have been observed at Bodega Head, but such temperatures much occur toward Cape San Lucas, Baja California, the southern limit of this species' range (Fritchman, 1961). The fact that *A. scabra* prefers horizontal surfaces (Haven, 1970) and does not avoid sites fully exposed to the sun, suggests that in the southern portion of the geographical range mortality due to extreme environmental temperatures may set the upper intertidal distribution limit of this species. On the other hand, it seems unlikely that heat death will be found to limit intertidal distributions of the other species even at the southern range limits, in view of their ability to select tolerable microhabitats. It seems more likely that they would simply select increasingly protected roosting sites at lower latitudes. Geographical range limits in these species may be the result of reproductive failure, either in adult gametogenesis or larval survival, as concluded by Fritchman (1961) on the basis of gonad index cycles. Testing of this hypothesis must await the development of culturing techniques for adults, larvae, and settling stages of *Acmaea*, which has only begun (Kessel, 1964).

From the foregoing it is clear that high temperatures do not of themselves limit the intertidal distributions of *Acmaea* on Bodega Head. Nevertheless, several data implicate high temperatures as an important contributing factor. Exceptionally warm weather was associated with all of the limpet "kills" previously reported (Orton, 1933; Hodgkin, 1959; Frank, 1965a; Sutherland, 1970), and with most of those observed during the course of this study. Although small *Acmaea* do not have lower lethal limits than their larger brethren, Davies (1970) has reported that the small individuals of *Patella* reach the highest temperatures in the field. It is the small *Acmaea* that seems most susceptible during "kills" (Table VI).

One of the physical effects of increasing temperature is an increase in the vapor pressure of fluids, and hence in evaporation rates. Desiccation rate of *Patella* under laboratory conditions increases with decreased body size, and the same relationship seems to hold for *Acmaea* in the field (Table VI). In all cases of "kills," deaths were observed in the high intertidal after two or more days of warm weather. A hypothesis consistent with all of these data is that cumulative, eventually lethal desiccation is the "limiting factor" determining the partitioning of the intertidal by these five species of *Acmaea*. If this hypothesis is correct, again two criteria should be satisfied. First, the limpets should show interspecific differences in adaptation to drying conditions, permitting them to exist in microhabitats exhibiting differing degrees of desiccation potential. Secondly, desiccation should be found to at least occasionally cause mortality in the field, thus restricting ranges at different levels depending on the physiological tolerances. The first criterion is satisfied, since differences exist in both desiccation rates and desiccation tolerances. However, the second criterion is satisfied in only some of the species on Bodega Head.

Desiccation rates of *A. pelta* and *A. t. scutum* are significantly higher than those of the Zone I species under mildly drying conditions (Table V). A similar pattern was found among British limpets by Davies (1969); high-shore *Patella*

vulgata show lower desiccation rates than low-shore *P. vulgata* or *P. aspera*. Unfortunately actual rates cannot be compared between the two studies because Davies exposed his limpets to dry, still air in desiccators, whereas moving air was used in the present study. Increasing the severity of drying conditions causes a proportionately greater increase in the rates of the Zone II *Acmaea*; under conditions common in Zone I on warm days, Zone II limpets may desiccate up to 11 times faster than Zone I limpets (Table V, column 2).

Three characteristics of the limpets were examined as possible mechanisms of the interspecific differences in desiccation rates: body size, shell shape, and the production of a mucus sheet between shell margin and rock. Size does appear to be an important factor in intraspecific variation in desiccation rate. Small specimens of *A. digitalis* are less tolerant of prolonged drying than are larger individuals (Frank, 1965a) and smaller individuals of *Patella vulgata* and *P. aspera* have higher rates (integrated evaporation-limited and diffusion-limited) of water loss (Davies, 1969). Desiccation of limpets under constant conditions on Mylar discs showed no clear relationship between size and diffusion-limited desiccation rate, although small animals apparently do desiccate faster in the field (Table VI). These data suggest that the size effect is most pronounced during the early evaporation-limited (Fig. 2) drying of the surface and immediately underlying tissues. In smaller limpets this involves a larger proportion of the total water; consequently, its more rapid loss gives desiccation a "head start" and leads to earlier mortality under prolonged exposure.

However, size differences and the attendant surface-volume relationships do not account for the observed interspecific differences in desiccation rates. *Acmaea pelta* and *A. persona* fall into roughly the same size range, yet have widely disparate desiccation rates. On the other hand, *A. digitalis* and *A. scabra* are smaller and thus have higher surface-to-volume ratios than *A. pelta* or *A. t. scutum*, yet have much lower rates.

Shell shape is not the determining factor either. *Acmaea testudinalis scutum* is considerably flatter than the other species, thus having a greater relative circumference, hence a longer aperture through which water vapor may escape, and shows the highest desiccation rates (Table V). However, *Acmaea persona* and *A. pelta* have virtually identical relative circumferences, yet *A. pelta* loses water much more rapidly. Furthermore, even the greatest differences in shell circumference (about 25%) are insufficient to account for the differences in desiccation rate observed between Zone I and Zone II limpets.

The ability to form a mucus sheet between shell margin and substrate (Fig. 3), which occurs in the species with low desiccation rates, is by far the most important adaptation. Removal of an intact sheet increases the desiccation rate by approximately seven fold (Fig. 5), causing *A. digitalis* without its mucus sheet to lose water at approximately the same rate as would *A. pelta* under the same conditions (Table V). It appears that this single mechanism accounts for almost the entire difference between desiccation rates of Zone I and Zone II limpets. It is further indirect evidence of the adaptive value of the mucus sheet that the limpets will repair one that has been damaged or obliterated, despite the short-term sacrifice of considerable water. *Acmaea digitalis* replaced completely destroyed mucus sheets up to five times, becoming incapable of doing so when more than 35% of the total water had been lost.

The mucus sheet lowers the desiccation rate of *A. digitalis*, which does not fit the rock, to the same level shown by *A. scabra* having an almost perfect fit of shell to rock (Table V; Fig. 5). Thus the effect of "homing" is not to give *A. scabra* a much lower desiccation rate than possessed by any other species, as has been suggested by Haven (1970). Thus the function, as well as the mechanism, of this complex behavioral phenomenon have yet to be adequately explained, in spite of copious research (Russell, 1907; Pieron, 1909; Wells, 1917; Orton, 1929; Abe, 1940; Hewatt, 1940; Villee and Groody, 1940; Edelstan and Palmer, 1950; Thorpe, 1963 (review); Funke, 1964; Galbraith, 1965; Cook, Bamford, Freeman and Teideman, 1969; Thorne, 1969). The homing habit restricts *A. scabra* to the area within which it can forage and return to its homesite during a single tidal immersion. In contrast, *A. digitalis* and *A. persona* do not require a homesite for minimal desiccation rates, and *A. digitalis* is known to lead a more opportunistic existence, moving with seasonal changes in food and exposure (Frank, 1965a). If the reduction in mobility required by homing is a disadvantage, as seems logical, it presumably must be balanced by some unique advantage. Many *A. digitalis* which by virtue of their mucus sheets already have low desiccation rates, and a few *A. pelta*, which do not, have been observed to home on Bodega Head. This suggests that the advantage of homing may be primarily related not to desiccation but to some other environmental factor, e.g., dislodgement by wave impact or injury by water-borne sand swept under the shell margin.

Adaptive differences are also evident in the desiccation tolerances of the five species. Under mild desiccating conditions the Zone I limpets will tolerate loss of about 80% of their total water, while the Zone II limpets will tolerate loss of about 70%. Evaporative loss of such a large proportion of the total water must have profound osmotic implications, unless the limpets have some means of maintaining their internal concentration below that of the extra-corporeal water as it becomes concentrated by evaporation. Regulation of blood concentration does not occur; equilibration with solutions of high salinity is rapid (Fig. 8). An ability to displace some excess electrolytes from the cells, by accumulating amino acids or other organic solutes during hyperosmotic stress, exists in some molluscs (e.g., *Tegula funebralis*; Peterson and Duerr, 1969). Although in this study no analyses of the intracellular fluid compartment were made, the absence of excess chloride in the urine (Fig. 1) over that predicted for evaporation from an ideal salt solution suggests that in *Acmaea* no such mechanism exists. This implies that concentration of the extra-corporeal water must result in a similar increase in electrolyte concentration of the blood and even of the intracellular fluid.

If it is the osmotic effects of desiccation which are crucial, then the apparently minor differences in desiccation tolerances—from about 70% total water lost in the Zone II species to about 80% in the Zone I species—are not so minor. The osmotic concentration of body fluids resulting from desiccation is not proportional to the per cent water lost, but to the inverse of the per cent water remaining. Hence, the internal osmotic concentrations corresponding to the lethal desiccation limits (Table VII) range from about 280–380% sea water for Zone II limpets to 450–550% sea water for the Zone I limpets—a substantial difference indeed.

The osmotic concentrations corresponding to desiccation tolerances are closely paralleled by the osmotic tolerances determined by 5-hour immersion in hyperosmotic solutions: Zone II limpets tolerate up to 400% sea water; a majority of Zone I

limpets survive up to 600% sea water. The slightly higher tolerances during immersion are presumably due to the shorter exposure to osmotic stress—5 hours during immersion *vs.* 1–8 days during the course of desiccation.

All of these limpets are remarkably tolerant of both desiccation and osmotic extremes. Their desiccation tolerances are comparable to those of some chitons (75% total water lost; Boyle, 1969), and are higher than those reported by Davies (1969) for *Patella* (30–65%). The desiccation tolerances of *Acmaea* are among the highest recorded for any animals, including desert amphibians (60% total water lost in *Scaphiopus*; Thorson and Svihla, 1943) and desert insects (55% total water lost in tsetse flies; Bursell, 1959). The ability of larval chironomids (*Polypedilum vanderplanki* from African desert rockpools) to survive complete desiccation (Hinton, 1950) of course represents the ultimate in adaptation along this line, but renders the tolerances of the essentially marine limpets only slightly less impressive. The range of external, and hence internal and intracellular concentrations tolerated by all five species—30% to 400% sea water—is also extremely wide when compared with published tolerances of other euryhaline molluscs. Among the hardiest are the intertidal estuarine mussel *Modiolus* (8.5–137% sea water; Pierce, 1970); the intertidal pulmonate *Siphonaria* (31–230% sea water; Allanson, 1958); the intertidal chiton *Sypharochiton* (50–150% sea water; Boyle, 1969); and the ventricle-strip preparation from the mussel *Mytilus* (10–200% sea water; Pilgrim, 1953). It must be borne in mind, however, that most of these studies of osmotic tolerances involve extended exposures (*e.g.*, 60 days; Pierce, 1970); the administration of fresh water or 400–600% sea water for such lengthy periods would represent a highly unnatural situation. The possibility of extreme osmotic fluctuations occurring during relatively short periods, as might happen in exposed animals during tidal emersion, appears to have been overlooked. Thus, with the exception of data for *Sypharochiton* (tolerates 75% total water lost, equivalent to 400% sea water; Boyle, 1969) and *Siphonaria* (tolerates 225% sea water for short periods; Allanson, 1958), few strictly comparable measurements of osmotic tolerances are available for other molluscs.

In addition to the differences in absolute tolerances of desiccation and its osmotic effects, there are differences in the duration of stressful conditions that the limpets will survive. *Acmaea digitalis*, *A. scabra*, and *A. persona* under mildly drying conditions (18° C, 68% R.H., 1.4 m/sec airflow) survived up to eight days. On the other hand, *A. scutum* experienced 100% mortality by the second day of exposure to even less severe conditions, before high levels of desiccation had been reached. Apparently the Zone II species will not tolerate drying conditions for periods much in excess of 24 hours. Similarly, Zone I limpets will tolerate 400% sea water for several days, whereas Zone II limpets succumb within 22 hours (Fig. 9).

The ability of the Zone I limpets, especially those of small size, to tolerate desiccation and its osmotic effects for such extended periods has been attributed to stores of extra water held under the shell. The relative water-holding capacity of the shell is larger in smaller limpets (Abe, 1931; Segal, 1956a); and water-holding capacity or "extra-visceral space" is larger in high intertidal species of *Acmaea*, or high-intertidal subsamples within species (Shotwell, 1950a; Segal, 1956a). Segal and Dehnel (1962) found that removing the "extra-visceral water" (mantle-

cavity water and voided urine, more accurately "extra-corporeal water") from *A. limatula* before subjecting the limpets to desiccation in the field slightly accelerated concentration of body fluids. However, the maximum difference between concentrations in the experimental animals and the controls was only about 13%, and had virtually disappeared after four hours, when the blood concentrations of both groups had not risen beyond 120% sea water. Segal and Dehnel concluded from these data that the extra-corporeal water performs a significant function in retarding desiccation. However, the transient delay in concentration of body fluids appears to be a small difference compared with the duration of desiccation and the levels of osmotic concentration which are likely to be stressful. Segal and Dehnel's data show that *A. limatula* easily tolerates 150% sea water for 48 hours, and all five species of *Acmaea* in this study would tolerate 400% sea water for the entire duration of Segal and Dehnel's desiccation experiment.

Segal (1956a) and Segal and Dehnel (1962) refer to the extra-corporeal water as though the limpets could expend this store before they were obliged to sacrifice body water; in such a compartmentalized situation the augmentation of the extra-corporeal water might serve an important function in delaying concentration of body fluids. However, it has been shown that there is no osmotic barrier between the extra-corporeal water and body fluids (Fig. 7; Segal and Dehnel, 1962; Webber and Dehnel, 1968). Therefore, it is not the amount of water stored in the "extra-visceral space," but the total amount of water stored under the shell, including body water, that is the significant measure of osmotic buffering ability. Increases in water-holding capacity are significant only if they result in increased water-holding. This is not the case in the Zone I species of *Acmaea*, which actually retain a few per cent *less* water than *A. pelta* and *A. t. scutum* (Table VIII). Neither do the small limpets hold relatively more water than the large ones (Table VIII). Observations show that, shell capacity notwithstanding, limpets expel or resorb most of the extra-corporeal water within the first few hours of desiccation under laboratory conditions. It therefore seems that "adaptive differences" in water-holding capacity are a laboratory artifact and are unimportant in delaying the desiccation of small or high-intertidal limpets. The observed differences in desiccation tolerance must therefore involve not morphological differences, but differences in physiological adaptation to some potentially lethal effect of desiccation.

There is a striking parallel between desiccation tolerances and osmotic tolerances. However, the question remains whether evaporative concentration of body fluids is what leads to death during desiccation, or whether some other effect of desiccation supervenes. Accumulation of toxic anaerobic metabolites during exposure, as may occur in the barnacle *Chthamalus* (Barnes and Barnes, 1964), is unlikely in *Acmaea* since the limpet continues to take up oxygen via the mantle fold during exposure (Baldwin, 1968; Kingston, 1968). Work on other intertidal molluscs suggests that such aerial respiration is common; it may be lower (Helm and Trueman, 1967; Lent, 1968; Paine, 1971) or higher than respiration while submerged (Micallef and Bannister, 1967, Sandison, 1968) but is reduced as desiccation progresses (Sandison, 1966). Irreversible damage to the respiratory surfaces by drying does not appear to be the direct cause of death, since limpets observed to have dried, stiff integuments often survived. Nor does lack of water as a biological solvent appear to be the cause of mortality as is im-

plied by McAlister and Fisher (1968) for the false limpet *Siphonaria pectinata*. Immersion of limpets in hyperosmotic solutions causes much less dehydration than does desiccation to the same internal concentration. Nevertheless, *A. t. scutum* and *A. pelta* die after less than 1.5 days exposure to a solution gradually concentrated to 250% sea water, just as they do if a similar rise in internal concentration is produced by desiccation with all of its attendant effects. The only stress common to the two experimental regimes is high osmotic concentration. No effects of desiccation, other than evaporative concentration, appear to cause death of limpets during drying; on the other hand, effects of osmotic stress associated with desiccation are sufficient to account for all desiccation-induced mortality. It therefore seems clear that the mechanism by which desiccation causes death in *Acmaea* is through concentration of the body fluids to lethal levels. The ability of the Zone I limpets to withstand severe, prolonged desiccation is a result of physiological adaptation to high electrolyte concentrations at the cellular level.

From the foregoing it is evident that interspecific differences in adaptation to drying conditions permit the observed partitioning of the intertidal zone by *Acmaea*. It is by virtue of their high desiccation tolerances, low desiccation rates, and ability to endure being in a desiccated state (or under hyperosmotic stress) for extended periods, that the Zone I limpets are able to exploit the otherwise inaccessible resources of the high intertidal. Their different mechanisms for achieving low desiccation rates dictate different life-styles. *Acmaea scabra* requires a close-fitting "homesite" to prevent rapid water loss; its foraging range is therefore limited to the area within which it can feed and return during a single tidal submersion—about 6 hours at best (Sutherland, 1970). *A. digitalis*, due to its ability to form the mucous diffusion barrier, is not dependent on a close fit to the rock, and is free to lead a more opportunistic existence. It seems to be able to outcompete *A. scabra* in most of Zone I (Haven, 1973), except in the most exposed, sun-baked sites. *A. scabra*, unlike *A. digitalis*, does not avoid these areas and, in part due to its adaptation to high temperatures, is able to exclusively exploit them. *A. persona* uses a third strategy, moving and feeding during the hours of darkness and hiding in crevices during the day; presumably this reduces competition with the other Zone I species in addition to lowering desiccation rates.

The Zone II limpets, however, do not have the physiological adaptations necessary for existence in Zone I. They lose water many times as fast as would Zone I limpets in similar circumstances (Table V); in addition, they have lower tolerances to desiccation and the resultant high internal osmotic concentrations (Table VII). The result is that, under conditions common in Zone I (Table V, column 2) they will reach their lethal limits in 6–10 hours. Furthermore, they are incapable of surviving in a desiccated state, or in a correspondingly concentrated salt solution, for more than 20–24 hours (Fig. 9). Thus, although this degree of adaptation allows *A. pelta* and *A. t. scutum* to survive in Zone II where exposure never exceeds 19 hours (Sutherland, 1970), they cannot survive in Zone I, where exposure may last up to 8 days. The upper range limits of these species may therefore be considered *potentially* limited by desiccation. However, they do not seem to ever attempt to migrate upward until stopped by their physiological limitations. No kills, or even near-lethal degrees of desiccation, have ever been observed in *A. pelta* or *A. t. scutum* in the field. Apparently the upper range limits of these

two species are not functionally determined by physical factors causing desiccation, but by behavioral adaptations leading to selection of physiologically tolerable microsites.

On the other hand, desiccation mortality does appear to have important effects on limpet populations in Zone I. Numerous specimens of *A. scabra* and *A. digitalis* have been found dead in the field on several occasions, usually after periods of unusually warm weather. Such kills seems to take a greater toll of small limpets (Table VI), presumably due to the greater surface-to-volume ratio and resultant higher initial rate of water loss. Characteristically, size distributions of limpets and other molluscs in the high intertidal are heavily skewed toward older individuals (Das and Seshappa, 1948; Frank, 1965a; Sutherland, 1970). This may very well be the result of higher desiccation mortality in smaller size classes, as suggested by North (1954) and Boyle (1970).

In each kill the dead limpets were found only at the upper limits of the species' intertidal ranges. The most extensive kill observed during the course of this study (11 August 1971) was preceded, not by heat, but by cool, foggy, almost windless weather. The sea had been exceptionally calm, and areas which normally receive abundant spray had been left dry for at least a week. Hundreds of limpets up to 11 years old (estimated from calculated growth curves in Frank, 1965b, and Sutherland, 1970) were eliminated from the upper reaches of these areas. Similar kills have eliminated limpet populations from high Zone I areas elsewhere on Bodega Head (Sutherland, 1970) as well as on Oregon (Frank, 1965a) and British coasts (Orton, 1933). Kills of *A. persona* have not been observed, possibly due to the scarcity of this species in the study area. However, desiccation-induced mortality obviously does set the upper range limits of *A. digitalis* and *A. scabra* on Bodega Head.

This brings us full circle to the question, "Do physical environmental conditions limit the ranges of animal populations?" Clearly they do in some cases. The physiological adaptations of *A. digitalis* and *A. scabra* to desiccating conditions permit their exploitation of Zone I, and desiccation mortality sets the upper limit of their ranges. However, it is equally clear that physical environmental conditions do not limit ranges in some other cases. Upper range limits of two otherwise very similar species, *A. pelta* and *A. t. scutum*, are determined by their behavior, not desiccation mortality.

As so often happens, one set of answers has led to another question: "Under what circumstances are physical factors likely to limit the ranges of animal populations?" It seems logical that animals which live in marginal habitats and are frequently pressed to the limits of their physiological endurance must expend a greater proportion of their energy coping with the environment, and in addition will not be able to compete effectively with similar animals physiologically better adapted to that habitat. The result is a decrease in the energy available for reproduction. Animals which are pressed beyond their physiological limits die, and of course lose all of their reproductive potential.

Natural selection, favoring traits increasing reproductive success, would be expected to exert pressures for both maximizing energy acquisition and minimizing mortality (the latter especially in limpets, where reproductive output increases markedly with increasing size and age). The result is a balance between selection

for exploitation of new resources by range extension, and selection for decreased risk of mortality by avoidance of marginally suitable range. Where the range overlaps with those of competing organisms, there is little energy to be gained by range expansion; the competing organisms presumably have a physiological advantage in that portion of the habitat. Under these conditions the balance of selection would be expected to favor behavioral adaptations resulting in occupation of physiologically more suitable portions of the range. However, where the habitat at and beyond the range limit of the species contains a resource unexploited by competing organisms, and opportunistic utilization of this resource increases reproductive success sufficiently to offset the risk of death, the balance of selection pressure will be shifted, from favoring stress avoidance to favoring range expansion.

This leads to the hypothesis that most species should be expected to be limited behaviorally, or by competition, to a range narrower than that in which their physiological tolerances would permit survival. Only those species whose range borders on an exploited resource might be expected to have extended their ranges to the limits of their physiological tolerances, and to be prevented from expanding them further by catastrophic mortality caused by physical factors. This hypothesis is supported by the data for *Acmaea*. The Zone II limpets *Acmaea pelta* and *A. t. scutum* are flanked above and below by other herbivorous gastropods, and do not appear to be limited by physical factors. On the other hand, the Zone I limpets *A. digitalis* and *A. persona* are flanked above in seep areas by a thick algal carpet, and appear to be exploiting this resource to the limit of their hypo-osmotic tolerances. In the remainder of the intertidal, *A. digitalis* and *A. scabra* are flanked above by a visible algal film and virtually no competitors; here they are limited by physical environmental factors causing desiccation.

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SUMMARY

1. This study tests the hypothesis that physical factors limit the ranges of five species of limpets (*Acmaea*) inhabiting the splash zone (Zone I) and upper mid-tidal (Zone II) of the Central California rocky shore. Two criteria are considered necessary to establish the hypothesis. First, interspecific differences in adaptation to physical factors must permit exploitation of different portions of the intertidal gradient. Secondly, physical conditions, by occasionally causing mortality, must set the limits of ranges at different levels depending upon the interspecific differences in physiological tolerances.

2. Dilution by winter rainwater runoff probably presents no osmotic threat to *Acmaea*. No pronounced differences are evident in either resistance to or tolerance of dilution. All five species tolerate immersion in fresh water for periods in excess of the maximum exposure expected in nature. Under exceptional circumstances some Zone I limpets may experience entrapment and lethal dilution in fresh water seeps.

3. Interspecific differences in tolerance to high temperatures are clearly correlated with solar heating occurring in the species' natural microhabitats. Thermal tolerances show no pronounced seasonal acclimation or intraspecific variation in limpets from different zones.

4. During three years, maximum field temperatures never exceeded the thermal tolerance of any of the limpets. Furthermore, all of the species tested, with the exception of *A. scabra*, seem to avoid maximally exposed microhabitats. It is concluded that high temperatures do not of themselves limit distributions of these limpets, but contribute to desiccation.

5. The Zone I limpets show higher desiccation tolerances and will tolerate drying conditions much longer than Zone II limpets. The limpets have no mechanism for avoiding the osmotic effects of desiccation; as expected, the Zone I limpets also have higher tolerances to hyperosmotic solutions and will tolerate elevated concentrations longer than will Zone II limpets.

6. Tolerances of desiccation and of hyperosmotic solutions in all 5 species are extremely high, ranging from about 70% to about 82% total water lost, and from 400% to 600% sea water.

7. Mortality during desiccation can be attributed entirely to the concentration of internal fluids resulting from evaporative water loss. Contrary to earlier reports, there are no increased water reserves in Zone I limpets. Thus high desiccation tolerances depend on adaptation to high electrolyte concentrations at the cellular level.

8. Desiccation rates of Zone I limpets are as low as $\frac{1}{10}$ those of Zone II limpets. The reduction is due almost entirely to a mucous diffusion barrier produced between the shell margin of Zone I species and the substratum. Non-"homing" *A. digitalis*, by virtue of the mucus sheet, have the same desiccation rate as "homing" *A. scabra*, suggesting that the principal advantage of homing may not be desiccation resistance alone.

9. Environmental conditions in Zone I exceed tolerances of the Zone II limpet species, and therefore potentially limit their ranges. However, behavioral adaptations apparently prevent upward migration and occupation of potentially lethal microhabitats. Hence, although differences in adaptation to drying conditions exist, the second criterion is not satisfied, and desiccation is not considered limiting for Zone II *Acmaea*.

10. The greater adaptation of Zone I limpets to drying conditions permits their exploitation of the high intertidal. Furthermore, desiccation does kill *A. digitalis* and *A. scabra* high in Zone I, especially small individuals, during periods of unusually warm weather or reduced splash. Thus, desiccation mortality does limit upper ends of intertidal ranges and apparently influences age structure in populations of these species.

11. The hypothesis is advanced that in general, range limits of animal popula-

tions should not be expected to be limited by physical factors, but by behavior, competition, or some other biotic factor. Only where the range borders on an unexploited resource would selection pressure favor range expansion to the limits of physiological tolerances. The data presented for *Acmaea* support this hypothesis: the Zone II species, with ranges overlapping those of the Zone I limpets above, are limited by behavior; the Zone I species, bordered above by a visible algal film, are limited by desiccation.

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